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ABSTRACT

This study addresses glume absence in tribe Orcuttieae. In *Orcuttia californica, O. inaequalis,* and *O. viscida,* all spikelets possess two glumes except for the terminal spikelet of the inflorescence, which lacks both glumes. In *O. pilosa* and *Tuctoria greenei* the terminal spikelet lacks only the first (proximal) glume, whereas in *O. tenuis, T. fragilis,* and *T. mucronata* both glumes are developed on all spikelets. This is the first report of glume absence in species of Orcuttieae other than *Neostapfia colusana,* which has been long reported to lack both glumes on all spikelets. A hypothesis of phylogenetic relationships in the tribe is presented and characters involved are discussed. We hypothesize *Neostapfia* to be sister to a *Tuctoria/Orcuttia* clade, and *Tuctoria* to be a grade leading to a monophyletic *Orcuttia.*

Key words: glume absence, *Orcuttia,* Orcuttieae, *Neostapfia,* phylogeny, *Tuctoria.*

The grass tribe Orcuttieae are noted for their morphological and ecological specialization (Crampton 1959; Reeder 1965, 1982; Griggs 1976; Keeley 1998*a*) and rarity (Reeder and Reeder 1980; Skinner and Pavlik 1994). This unusual group of annuals is distinct from all other grasses: plants are beset with glands that produce a viscid, aromatic exudate, and the leaves are eligulate, without distinction into sheath and blade, and bear small, sunken, mushroom-button-shaped bicellular microhairs (Reeder 1965). Although the tribe is confidently placed in subfamily Chloridoideae (Stebbins and Crampton 1961; Reeder 1965), its closest relatives have yet to be identified. The many-nerved (7–17) lemmas led Stebbins and Crampton (1961) to place the species in tribe Pappophoreae, a relationship that is unlikely in light of other data (Reeder 1965). *Distichlis* Rafin. and *Eragrostis* N. M. Wolf have been suggested as potential close relatives (Columbus pers. comm. in Keeley 1998*a*), but discovery of the elusive sister group awaits molecular phylogenetic study.

In a taxonomic revision of the Orcuttieae, Reeder (1982) recognized three genera and nine species: *Neostapfia colusana* Davy, *Orcuttia californica* Vasey, *O. inaequalis* Hoover, *O. pilosa* Hoover, *O. tenuis* A. S. Hitchc., *O. viscida* (Hoover) J. Reeder, *Tuctoria fragilis* (Swallen) J. Reeder, *T. greenei* (Vasey) J. Reeder, and *T. mucronata* (Crampton) J. Reeder. Prior to this treatment, the three *Tuctoria* species were positioned in *Orcuttia.* All of the species are endemic to vernal pools of the California Floristic Province except *T. fragilis,* known only from a single desert playa in southern Baja California Sur, Mexico.

While examining plants of *Orcuttia californica* grown up from germination trials at Rancho Santa Ana Botanic Garden, we discovered that both glumes were lacking from the terminal spikelet in all inflorescences. All other spikelets, however, were observed to possess the normal pair of glumes. Herbarium specimens at RSA were then studied to ascertain the extent of this dimorphism. From this survey we report the following findings. In *Orcuttia californica, O. inaequalis,* and *O. viscida,* all spikelets possess two glumes except for the terminal spikelet of the inflorescence, which lacks both glumes. In *O. pilosa* and *Tuctoria greenei* the terminal spikelet lacks only the first (proximal) glume, whereas in *O. tenuis, T. fragilis,* and *T. mucronata* both glumes are developed on all spikelets. This is the first report of glume absence in species of Orcuttieae other than *Neostapfia colusana,* which has been long reported to lack both glumes on all spikelets. Interestingly, *Neostapfia* can have glumes present in the spikelet, as discussed in the original description by Davy (1898). He notes, "The 2 or 3 uppermost spikelets are subtended by linear or lanceolate linear empty glumes." When specimens are critically studied, this is indeed the case, with the addition that glumes may also be present on the lowermost spikelets of the inflorescence. It is clear that these bracts are indeed glumes and not foliacious bracts of the inflorescence, as they are positioned on the lateral spikelet axis, not the main axis.

It was then discovered that glumes are absent in those species with more congested inflorescences. The terminal spikelet in the dense, capitate inflorescence of *Orcuttia inaequalis* lacks both glumes, whereas the widely spaced spikelets of *O. tenuis* all have two

Table 1. Characters mapped on the phylogenetic tree. These characters are from Metcalfe (1960), Reeder (1965, 1982), and Keeley (1998a, b).

Character number	Character changes
1	Loss of ligule
2	Many-nerved lemmas (7–17 vs. 3)
3	Gain of glands
4	Gain of malate deposition in leaf glands
5	Gain of small, sunken, mushroom-button-shaped bicellular microhairs
6	Loss of embryonic epiblast
7	Gain of long, ribbon-like floating juvenile leaves
8	Loss of stomata on submerged juvenile leaves
9	Gain of lacunae in submerged juvenile leaves
10	Loss of kranz anatomy in submerged juvenile leaves
11	Increase in number of cells (5–7 vs. 1–3) between vascular bundles in submerged juvenile leaves
12	Gain of NADP-malic enzyme catalyzed decarboxylation

glumes. These species represent the extremes in inflorescence form. Griggs (1976) considered the inflorescence morphology of seven *Orcuttia* and *Tuctoria* species in context of pollination. His quantification of inflorescence density, as a percentage of the inflorescence axis bearing spikelets, serves to illustrate the relationship between inflorescence density and presence/absence of glumes in the terminal spikelet: *O. inaequalis,* 22% (0 glumes); *O. viscida,* 42% (0); *O. californica,* 48% (0); *O. pilosa,* 55% (1); *T. greenei,* 64% (1); *T. mucronata,* 70% (2); and *O. tenuis,* 81% (2). *Tuctoria fragilis,* not included in Griggs (1976) study also has two glumes on the terminal spikelet.

Employing characters extracted from Metcalfe (1960), Reeder (1965, 1982), and Keeley (1998a, b) (Table 1), we estimated the phylogeny of Orcuttieae intuitively (Fig. 1). It should be noted that only *Neostapfia, O. californica, O. greenei,* and *T. greenei* have been examined for characters 4, 8, 9, 11, and 12 (all from Keeley 1998a), but an assumption was made that all congeners are the same with respect to these characters. Although the sister group of the Orcuttieae has yet to be identified, characters were confidently polarized based on the rare suite of characters states found in the tribe with respect to the other members of Chloridoideae. These data suggest that *Neostapfia* represents the sister lineage to the *Tuctoria/Orcuttia* lineage and *Orcuttia,* by virtue of its numerous synapomorphies, is monophyletic. The conclusion regarding the position of *Neostapfia* was the same reached by Keeley (1998a), who employed the genera as terminal taxa in a cladistic analysis. While we have only coded one character (12) that separates *Neostapfia* from the rest of the Orcuttieae, there is other evidence for this position, though less convincing. *Tuctoria* is known to have intermediate states between *Neostapfia* and *Or-*

cuttia. The most notable are the number of juvenile submerged leaves, the RUBISCO:PEP carboxylase ratio, and germination time. These characters help to intuitively place *Tuctoria* between *Neostapfia* and *Orcuttia.* Unlike *Orcuttia,* monophylesis of *Tuctoria* is doubtful. Evidence that *Tuctoria* may represent a grade (i.e., paraphyletic genus) instead of a monophyletic group primarily involves chromosome number. Reeder (1982) reported a diploid chromosome number of 40 for *Neostapfia, T. fragilis,* and *T. mucronata,* whereas *T. greenei* and all *Orcuttia* species have fewer chromosomes, ranging from 24 to 30 (Fig. 1). There are no known synapomorphies for *Tuctoria.*

Characteristics of the lodicules in the Orcuttieae have become confused in recent literature. One of the characters used in the recent phylogenetic analysis of the Orcuttieae (Keeley 1998a) is lodicule reduction. Keeley characterizes the lodicules of *Tuctoria* as being reduced relative to *Neostapfia.* In the revision of the tribe, Reeder (1982) suggests that lodicule size varies among the *Tuctoria* species, and there is no clear reduction in size from *Neostapfia* to *Tuctoria.* In addition, the character "lodicules fused" used by Keeley (1998a) for *Tuctoria* is problematic. This is referring to fusion of the lodicules to the palea (not each other), and is also suggested to be variable for the genus (Reeder 1982). *Tuctoria mucronata* has lodicules fused to the palea, but in *T. fragilis* the lodicules are only "slightly" fused to the palea, and fusion of lodicules and palea is not addressed for *T. greenei* in Reeder's revision (1982), implying no fusion at all. Given these contradicting reports, more detailed study of lodicule variation is necessary.

In light of the foregoing phylogenetic hypotheses, the loss or gain of glumes appears to have occurred several times independently. Given that spikelets of all but a few other members of Chloridoideae possess both glumes, it is more likely than not that the common ancestor of the Orcuttieae bore glumes, and that glume development was subsequently arrested to varying degrees in several lineages. Although the tribe is predisposed to glume suppression, the complete absence of glumes in *Neostapfia* is a situation considerably different from that in the five other species lacking glumes, wherein only the terminal spikelet of the inflorescence is involved.

As can be seen from Fig. 1, the topology of the cladogram was not resolved solely from the characters listed in Table 1, but by considering inflorescence congestion (Griggs 1976), glume absence, and chromosome numbers (Reeder 1982) as well. We placed *Tuctoria greenei* as the sister species of *Orcuttia* because of its nontetraploid chromosome number. Arrangement of the *Orcuttia* species, however, was based on glume absence and inflorescence congestion, which do not correlate with chromosome number.
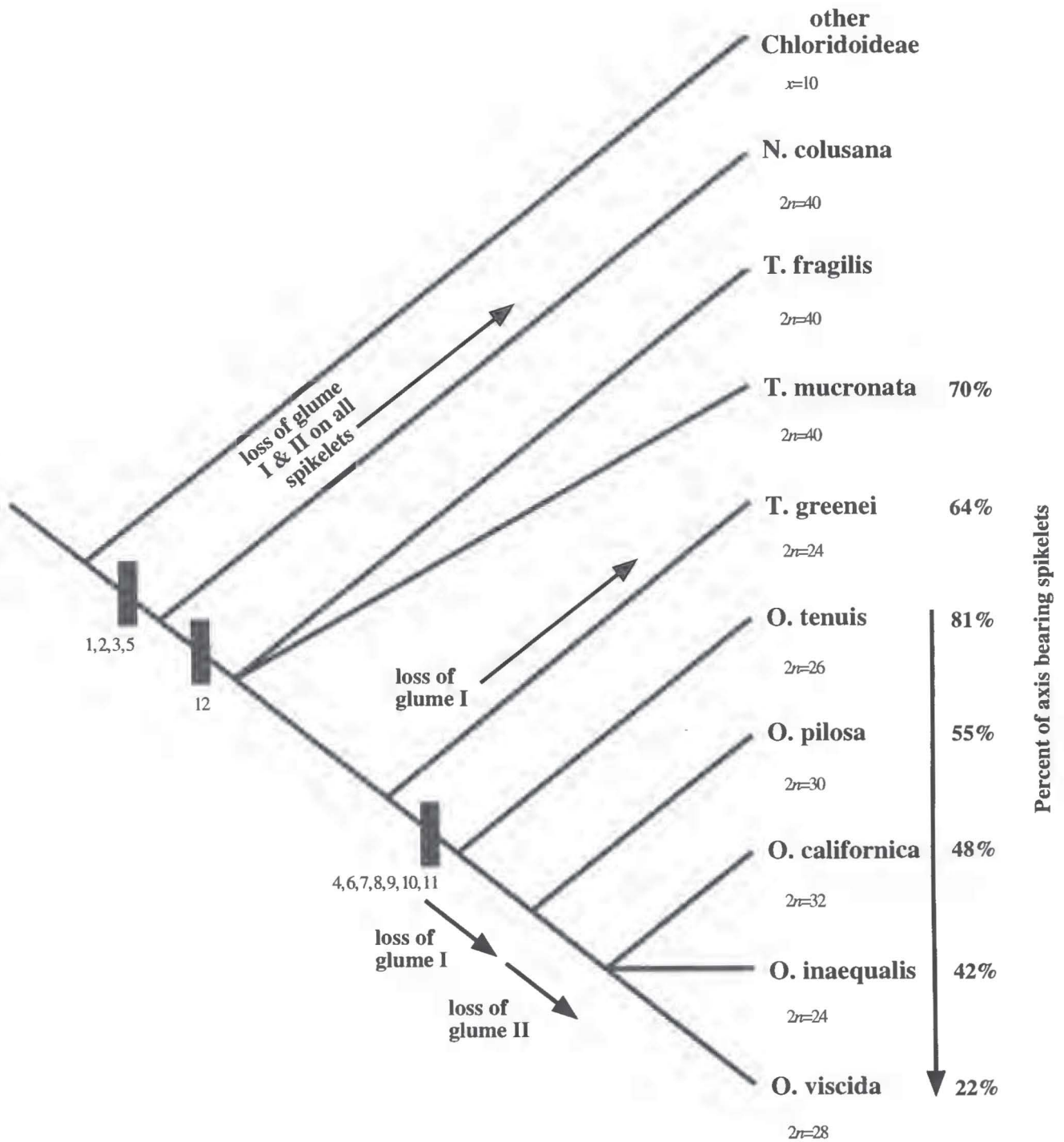
Fig. 1. Phylogeny of the Orcuttieae tribe. Glume loss arrows refer to the terminal spikelet in *Tuctoria* and *Orcuttia*. Character states of the outgroup (Chloridoideae) reflect the common state for other members of the subfamily. Chromosome numbers are from Reeder (1982), and percentage of axis bearing spikelets values are from Griggs (1976).

This hypothesis of interspecific relationships serves as the starting point for future phylogenetic work in the Orcuttieae. The study by Keeley (1998a), which provided a number of useful anatomical/physiological characters, should be expanded to include all species. Also, our understanding of the evolution of the tribe would likely be improved by employing molecular approaches.

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